

Yield and Water Use Response of Cuphea to Irrigation in the Northern Corn Belt

R. W. Gesch,* B. S. Sharratt, and K.-I. Kim

ABSTRACT

Cuphea (*Cuphea viscosissima* Jacq. × *C. lanceolata* W.T. Aiton) may be prone to drought stress, yet little is known about the yield response of this new oilseed crop to irrigation. A field study was conducted in western Minnesota on a Barnes loam soil (fine-loamy, mixed, superactive, frigid Calcic Hapludolls) in 2002 and 2003 to compare yield and water use of irrigated and nonirrigated cuphea. Nonirrigated cuphea received only precipitation, while irrigated plants received supplemental watering to maintain soil water content near field capacity during the study. Crop drought stress was assessed by measuring photosynthesis, stomatal conductance, leaf water potential, and $\delta^{13}\text{C}$ ($^{13}\text{C}/^{12}\text{C}$ stable isotope composition). In 2002, soil water content was similar for irrigated and nonirrigated plants throughout the growing season owing to timely rains, and seed yield was similar between treatments (873 kg ha^{-1}). During 2003, irrigation resulted in a 2.7-fold increase in seed yield and greater harvest index than nonirrigated plants, while water use efficiency (WUE) of seed production for both treatments was similar ($2.4 \text{ kg ha}^{-1} \text{ mm}^{-1}$). Drought conditions occurred in 2003; by mid-August, leaf photosynthesis and leaf water potential of nonirrigated plants were 83 and 56% less, respectively, than for irrigated cuphea. Moreover, $\delta^{13}\text{C}$ measurements of seed further confirmed that nonirrigated cuphea suffered significant drought stress. Our results indicate that cuphea is drought sensitive and that regions or soils prone to water deficits will likely require supplemental irrigation to increase seed yield.

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Abbreviations: AWHC, available water-holding capacity; ET, evapotranspiration; GDD, growing degree days; RZ, rooting zone; WFBRZ, water flow below the root zone; WU, water use; WUE, water use efficiency.

CUPHEA (*Cuphea viscosissima* Jacq. × *C. lanceolata* W.T. Aiton) is a new oilseed crop being developed as a source of medium-chain triglycerides. The cultivar PSR23, which shows the greatest agronomic potential, is an interspecific hybrid developed from crossing *Cuphea viscosissima* and *C. lanceolata* (Knapp and Crane, 2000). PSR23 is particularly rich in capric acid (Forcella et al., 2005), which has several important uses in the chemical manufacturing industry (Thompson, 1984). Cuphea seed oil also shows exceptional potential as an engine lubricant (Cermak and Isbell, 2004) and biofuel (Johnson et al., 2007). As with any newly developed crop, gaining a better understanding of agronomic inputs to minimize physiological stresses associated with soil and climate conditions will aid in optimizing production as well as identifying regions best suited for production.

Previous research has shown that PSR23 cuphea grows well in the northern Corn Belt region of the United States (Gesch et al., 2006). In a 2-yr study conducted at seven different field sites, ranging from southwest Iowa to northwest Minnesota along a predominately 95.5 to 96°W longitude, Forcella et al. (2005) showed that cuphea seed yield generally increased with increasing latitude. Mean seasonal temperature and precipitation during their study indicated that the likelihood of drought stress was greater at sites in Iowa than in Minnesota. In fact, during the second year of their study, irrigation

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applied (amount of water not measured) at the two most southerly sites (Lewis and Castana, IA) resulted in a doubling of yield over nonirrigated plants. The authors pointed out, however, that although soil moisture was certainly a factor contributing to yield differences, it could not fully explain differences in yield across all sites in their study. Other possible reasons cited for yield differences included higher growing season temperatures at southerly latitudes that might have hindered reproductive growth and potentially greater seed shattering at southerly sites related to more rapid plant development, although these factors were not specifically measured (Forcella et al., 2005). Differential availability of insect pollinators across research sites was another factor cited as a potential contributor to yield differences. PSR23 cuphea flowers are known to be strongly dependent on insect cross-pollination (Knapp and Crane, 2000; Forcella et al., 2005).

Other research evidence indicates that water is likely a very important limiting factor for cuphea production. Sharratt and Gesch (2004), studying the effects of row spacing and sowing date on water use and root-length density of cuphea in Minnesota, found that the effective maximum rooting depth of cuphea was about 0.6 m, with nearly 70% of the total root length located in the upper 0.2 m of the soil profile. Furthermore, they found that cuphea's water use efficiency of seed production, which ranged from 1.2 to 2.0 kg ha⁻¹ mm⁻¹ of water, was lower than that of most other oilseed crops. The authors suggested that, owing to its sparse, shallow root system combined with its rather low water use efficiency (WUE), cuphea might be prone to drought stress during the growing season.

Little information exists on the physiological and yield response of cuphea to supplemental water applications. Such information, however, would be useful in helping to determine the adaptability of cuphea to northern U.S. cropping systems and aid in developing better crop production management strategies. The objective of the present study was to use irrigation as a means to assess the yield potential and water use characteristics of cuphea under otherwise potentially soil-water-limiting conditions during the growing season.

MATERIALS AND METHODS

This study was conducted in 2002 and 2003 on a Barnes loam soil (fine-loamy, mixed, superactive, frigid Calcic Hapludolls) at a field site located 24 km northeast of Morris, MN (45°35' N, 95°54' W). Cuphea (PSR23) was planted 14 May in 2002 and 2003. In both years of the study, the previous crop was cuphea. The seedbed was chisel-plowed the previous fall and harrowed just before planting, at which time fertilizer was broadcast and incorporated into the soil at a rate of 112, 13, and 30 kg ha⁻¹ of N, P, and K, respectively. Cuphea was seeded at 40 kg ha⁻¹ on 20-cm-spaced rows at a depth of 6.4 mm with a no-till grain drill. After emergence, plants were thinned by hand to a population of 400,000 plants ha⁻¹.

The experimental design was a randomized complete block with irrigated and nonirrigated cuphea treatments replicated three times. Plot size was 6 × 6 m, and a drip irrigation system was

installed within a 3 × 3 m area in the center of each treated plot. Instrumentation to measure soil water content and matric potential was installed within this area immediately following sowing. Also, all plant sampling and measurements were made from the 3 m² area where the drip system was installed. Soil water content was measured at least weekly by neutron attenuation at depths of 0.15, 0.45, 0.75, and 1.05 m in each plot. Soil matric potential was measured with tensiometers placed at depths of 0.1, 0.3, 0.8, and 1.0 m in irrigated plots and at depths of 0.8 and 1.0 m in control (nonirrigated) plots. Tensiometers were monitored manually once per day on two different days each week.

The drip irrigation system was installed after plants had fully emerged in mid-June. Surface drip lines (15 drip lines per plot connected to a main watering line with 15 emitters per drip line spaced 20 cm apart) were installed between rows. The emitters had a water delivery rate of 24 mL min⁻¹. The main watering line was connected to a pressure regulator and motorized pump to deliver water; the system was pretested for water delivery before field installation. The amount of water required to recharge the majority of the rooting zone (RZ) of the soil profile to near saturation in irrigated plots was determined by:

$$WR = (FC - OBS) \times RZ \quad [1]$$

where WR is the water (m) required to recharge the RZ, FC is volumetric soil water content (m³ m⁻³) of the RZ near saturation (value of 0.34 m³ m⁻³, corresponding to a matric potential of -0.01 MPa), and OBS is the volumetric water content (m³ m⁻³) of the RZ at the time of each observation. The OBS water content was estimated using matric potential measurements and the water retention characteristics of the soil (i.e., volumetric water content vs. matric potential). We assumed a value of 0.3 m for RZ in this study, since previous work by Sharratt and Gesch (2004) showed that >80% of cuphea root-length density in a Barnes loam soil is found above this depth. Plots were irrigated when matric potential at either the 0.1- or 0.3-m depth was <-0.03 MPa. Thus, the objective was to maintain the upper 0.3 m of the soil profile in the irrigated treatment within a range of matric potential of -0.03 to -0.01 MPa. Although no previous studies have examined the yield response of cuphea to soil matric potential, yield of most crops is not compromised when soil matric potential is maintained above -0.03 MPa (Taylor and Ashcroft, 1972). During each irrigation, water was collected from each emitter located at the four corners of the drip system to determine the actual amount of water added to each irrigated plot. On average, the actual amount of water added was 93% ± 16% SD of the calculated target amount.

Water use (WU) was determined by

$$WU = P + I \pm \Delta SW - RO \pm WFBRZ \quad [2]$$

where *P* is precipitation, *I* is actual amount of water applied by irrigation, ΔSW is change in soil water content, *RO* is lateral surface water runoff, and *WFBRZ* is the water flow below the root zone. Water use was computed weekly and totaled for the season from emergence to harvest. Weekly neutron attenuation measurements at 0.15 and 0.45 m were used to determine ΔSW . Runoff was considered negligible because there were few intense rainfall events (rainfall did not exceed 30 mm except on 3 d in 2002 and 4 d in 2003), the topography of the site was relatively level, and no noticeable rills or washing of debris at the soil surface was observed following any rain event. Water flow

below the root zone was determined according to the methodology used by Sharratt and Gesch (2004). Briefly:

$$\text{WFBRZ} = -k(\Delta h/\Delta z) \quad [3]$$

where k is hydraulic conductivity (m s^{-1}) and $\Delta h/\Delta z$ is the difference in hydraulic potential (m) across the 0.8- to 1.0-m depth interval. Hydraulic conductivity was estimated from saturated hydraulic conductivity, soil water retention parameters, and soil matric potential according to Campbell (1985). In situ soil core samples were extracted from a depth of 1.0 m in cuphea plots located adjacent to our study to ascertain saturated hydraulic conductivity by the constant-head method (Klute and Dirksen, 1986) and soil water retention parameters, namely, air entry potential and slope of the water retention curve, using a pressure plate apparatus (Klute 1986). Climate data were measured at an automated weather station within 150 m of the study site. Potential evapotranspiration (ET_0) was calculated using daily weather station data and the FAO (Food and Agriculture Organization of the United Nations) Penman–Monteith equation (Allen et al., 1998) for a grass reference (short canopy, 0.12 m).

Leaf photosynthesis and leaf water potential were measured near midday on clear sunny days during the growing season from approximately 2 wk before flowering to full bloom and seed set (mid-August) in 2003. Photosynthesis and stomatal conductance were measured approximately once every 2 wk on the uppermost fully expanded sunlit leaf of six randomly chosen plants from each plot with a LI-6400 Portable Photosynthesis System (LI-COR, Lincoln, NE) between 1130 and 1300 h Central Standard Time (CST). The six measurements were averaged, and values reported are the overall mean of the plot averages by treatment. Measurements were made at or near ambient temperature under a CO_2 concentration of $380 \mu\text{mol mol}^{-1}$ and $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation using an artificial light source (6400-02B Red/Blue Light Source, LI-COR). Photosynthesis was measured on 2 July, 18 July, 4 August, and 18 August, during which time LI-6400 cuvette air temperatures were 33.2 ± 0.2 SD, 29.3 ± 0.5 , 29.8 ± 0.4 , and $34.9 \pm 0.9^\circ\text{C}$, respectively, during measurements. Leaf water potential was measured once a week until 1 August and then again 3 wk later on four randomly chosen, uppermost, fully expanded leaves between 1000 and 1130 CST using a portable Scholander pressure apparatus (Model 3005, Soil Moisture Equipment Corp., Santa Barbara, CA). Leaves were excised at the petiole base and immediately transferred to the pressure chamber to determine water potential. The four measurements were averaged, and values reported are the overall mean of the plot averages by treatment.

Seeds harvested in 2003 were analyzed for $\delta^{13}\text{C}$ on a 20–20 Europa ratio mass spectrometer (Europa Scientific, Cheshire, England). Approximately 110 mg of clean dry seed (30 to 40 individual seeds) from each treatment replication was ground with a mortar and pestle and 3 mg of this was used for analysis. The $\delta^{13}\text{C}$ values (‰) were determined by:

$$\delta^{13}\text{C} = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000 \quad [4]$$

where R_{sample} is the $^{13}\text{C}/^{12}\text{C}$ ratio of the sample and R_{standard} is the $^{13}\text{C}/^{12}\text{C}$ ratio of a standard calibrated to the PDB standard, a limestone fossil of *Belemnitella Americana* from the Cretaceous Pee Dee formation in South Carolina (O'Leary, 1993; Farquhar and Lloyd, 1993). Negative values indicate that $^{13}\text{C}/^{12}\text{C}$ ratio of the sample is lower than the PDB standard. Typical $\delta^{13}\text{C}$ values

for air, C_3 plants, and C_4 plants are -8 ‰, -27 ‰, and -13 ‰, respectively (Boutton, 1991).

Plants were hand-harvested from a 1 m^2 area in the center of each plot on 8 October in 2002 and 16 September in 2003. The plants were dried in a greenhouse maintained at average 27°C day– 21°C night temperatures before determining biomass, then threshed. Seed was screen-cleaned for determining yield. A subsample of seed from each plot was further dried at 60°C to constant weight to determine moisture content of yield samples, which averaged 5% (w:w).

The experimental data were analyzed by ANOVA using the GLM Procedure of SAS (SAS for Windows 9.1, SAS Inst., Cary, NC). Because there were significant differences between years caused by climatic variation, data was analyzed separately by year. Least significant differences at the $P = 0.05$ level were used to separate differences between treatment means.

RESULTS AND DISCUSSION

The growing seasons (i.e., May through September) of 2002 and 2003 were similar with respect to total precipitation and accumulated growing degree days (GDD) (Table 1). However, the distribution of precipitation and air temperature during the growing season greatly differed between years. For instance, from May through June, precipitation was 52 mm below the 120-yr average in 2002 and 74 mm above average in 2003, whereas from July through August it was 64 mm above average in 2002 and 95 mm below average in 2003. Mean monthly air temperature in 2003 was similar to that of the 120-yr average throughout the growing season, except for August, which was about 2.0°C above normal. In 2002, May was unusually cold (2.0°C below average) and August was near normal, but June, July, and September were about 2.0°C above the 120-yr average. Monthly cumulative reference ET (ET_0) for July and August was greater during 2003 than 2002.

Vegetative growth of cuphea proceeds rather slowly, but its growth rate increases sharply on entering reproductive phase, which varies with temperature (Gesch and Forcella 2007). Cuphea requires approximately 500 to 800 GDD to reach flowering in the northern Corn Belt (Gesch et al., 2002; Berti and Johnson, 2008a). For cuphea planted in west central Minnesota from late April through mid-May, flowering typically begins in mid-July (Gesch et al., 2002). During both years of the present study, cuphea began flowering between 15 July and 20 July (field observation). Because of cuphea's indeterminate growth habit, it continues to flower until killed by hard frost, but generally, greatest flowering occurs in late July through mid-August (Gesch et al., 2006). Physiological maturity of cuphea seed requires about 253 GDD, or about 28 to 30 d after pollination in the field (Berti and Johnson 2008b), while optimum harvest seed yield occurs by mid- to late September (Gesch et al., 2005). Therefore, late July through mid-September is a critical time in the life cycle of cuphea, when environmental stresses are likely to have their greatest impact on yield. Many agricultural grain crops are most sensitive to drought and high

Table 1. Monthly climate conditions for the 2002 and 2003 growing season. Accumulated growing degree days (GDD) were calculated using a base temperature of 10°C.

Year	Month	Mean air temp.	120-yr mean air temp. [†]	Deviation from mean	Precipitation	120-yr mean precipitation	Deviation from mean	GDD	ET _o [‡]
		°C			mm			°C d	mm
2002	May	11.5	13.5	-2.0	66.8	75.3	-8.5	77	125
	June	21.2	18.9	2.3	57.4	101.0	-43.6	316	150
	July	23.3	21.6	1.7	147.1	93.2	53.8	397	134
	August	20.2	20.4	-0.1	85.9	76.0	9.9	301	109
	September	17.0	15.1	1.9	29.0	58.7	-29.7	202	92
Total		—	—	—	386.2	404.2	-18.1	1293	610
2003	May	13.8	13.5	0.3	73.2	75.3	-2.2	98	118
	June	19.0	18.9	0.1	177.0	101.0	76.0	256	130
	July	21.8	21.6	0.2	64.5	93.2	-28.7	349	147
	August	22.3	20.4	1.9	9.9	76.0	-66.1	364	130
	September	14.8	15.1	-0.2	83.3	58.7	24.6	153	84
Total		—	—	—	407.9	404.2	3.6	1220	609

[†]Based on the 120-yr average monthly temperature and accumulated rainfall for the Morris, MN, location. Data were collected and compiled from the University of Minnesota West Central Research and Outreach Center, approximately 24 km from the study site.

[‡]Potential evapotranspiration (ET_o) was calculated for a grass reference (short canopy, 0.12 m) using daily weather station data and the FAO (Food and Agriculture Organization of the United Nations) Penman–Monteith equation.

temperature stress during reproductive growth, and this can lead to substantial yield loss (Barnabás et al., 2008).

Soil water content in the upper 0.6 m of the profile during the 2002 growing season was not significantly different between the irrigated and nonirrigated treatments (Fig. 1). Based on water retention characteristics of the Barnes loam soil (Cassel and Sweeney, 1974), volumetric water content of the upper profile at -0.03 MPa matric potential (field capacity) is 26% and at -1.5 MPa matric potential (permanent wilting point), 16%. Soil water content during 2002 ranged from 26 to 32% and 30 to 32% for the nonirrigated and irrigated treatments, respectively. Plant available water was therefore maintained near maximum available water-holding capacity (AWHC; the difference in water content between field capacity and permanent wilting point) of the soil. Thus, soil water likely did not limit plant growth for either treatment. Conversely, during 2003, soil water content in nonirrigated plots rapidly declined after 8 July and neared the permanent wilting point by 15 August (Fig. 1). Between 25 July and 12 September, plant available

water was depleted to below 50% of the AWHC of the soil. Although soil moisture in the irrigated plots declined slightly, plant available water never dropped below 60% of the AWHC. The trend in declining water content for the irrigated plots during the middle of the 2003 season (Fig. 1) was likely owing to plants extracting water from the 0.3- to 0.6-m depth that was not accounted for in our irrigation regime (Eq. [1]). For comparison, the water content in the 0- to 1.2-m soil profile during early vegetative growth of plants (late June) and at full bloom (mid-August) is shown in Fig. 2. In 2002, there was little change in soil water content throughout the profile between either the two growth periods or treatments. In 2003, although differences in soil moisture at the 0.15- and 0.45-m depths between treatments on 15 August were large and significantly different ($P < 0.05$), differences at the 0.75- and 1.05-m depths were not significant (Fig. 2). This can be attributed to the fact that the effective maximum rooting depth of cuphea is about 0.6 m (Sharratt and Gesch, 2004), thus resulting in greater water depletion at the shallower depths.

Table 2. Effect of irrigation on seed and biomass yield and seasonal water use characteristics of cuphea (*Cuphea viscosissima* Jacq. × *C. lanceolata* W.T. Aiton).

Treatment		Seed yield	Biomass	Harvest index	Water use	WUE [†] of seed production	WUE of total biomass production
		— kg ha ⁻¹ —			mm	— kg ha ⁻¹ mm ⁻¹ —	
2002	Nonirrigated	846 a [‡]	7104 a	0.090 a	365 b	2.3 a	21.8 a
	Irrigated	899 a	7699 a	0.089 a	522 a	1.7 b	16.5 b
2003	Nonirrigated	520 b	6636 b	0.072 b	221 b	2.4 a	32.6 a
	Irrigated	1400 a	10737 a	0.115 a	572 a	2.4 a	21.2 b

[†]WUE, water use efficiency.

[‡]Within a column for a given year, mean values followed by the same letter are not significantly different at the $P \leq 0.05$ level.

Crop water use was estimated from precipitation, water applied by irrigation, change in soil water content, runoff, and water flow below the root zone (Eq. [1]). Runoff was not apparent after intense rainfall events and, therefore, did not account for any water use during the 2002 and 2003 growing seasons. In addition, WFBRZ accounted for <1% of the total water use in 2002 and 2003. In 2002, there was a net upward movement of water (2×10^{-10} mm d⁻¹) into the root zone of nonirrigated cuphea and a net downward

movement of water (2×10^{-9} mm d⁻¹) below the root zone of irrigated cuphea. In 2003, there was a net upward movement of water (not greater than 2×10^{-9} mm d⁻¹) into the root zone of nonirrigated and irrigated cuphea. Based on these small water fluxes, we assumed WFBRZ was negligible and excluded WFBRZ from calculations of water use.

Seed yield, biomass, and harvest index were not affected by irrigation in 2002, but were in 2003 (Table 2). In 2002, total seasonal water use (WU) was less and WUE of seed and total biomass production were greater for nonirrigated plants. This was because ample amounts and timely distribution of precipitation were received during the growing season, especially during the critical period of July and August for flowering and seed development (Gesch et al., 2002; Gesch et al., 2005). Therefore, additional irrigation exceeded the water use necessary to maximize yield given other climate (e.g., temperature and humidity) and growth factors (e.g., soil nutrients). The average amount of supplemental water added to irrigated plots in 2002 was 140 mm, compared with 295 mm added in 2003.

Seed yield of irrigated cuphea in 2003 nearly tripled that of nonirrigated plants, and biomass yield was 62% greater (Table 2). Harvest index of irrigated plants was 60% greater than nonirrigated plants. Seed yield of nonirrigated plants was reduced to a greater extent than vegetative growth, which is why harvest index was markedly lower than for irrigated plants. This was caused by the hot and unusually dry conditions experienced during late summer of 2003 (Table 1 and Fig. 1). It has been suggested that PSR23 cuphea might be susceptible to drought because of its shallow root system (Sharratt and Gesch 2004), and moreover, reproductive growth of cuphea is considerably more sensitive to high temperatures than vegetative growth (Gesch and Forcella, 2007).

Despite adequate soil moisture in 2002, seed and biomass yields were lower than those of irrigated plants in 2003, suggesting that other factors besides water (e.g., disease and soil fertility) limited yield in 2002. We are not entirely sure why yields were lower in 2002. However, one potential reason is that there might have been differences in seed loss between years owing to seed shattering. Cuphea is prone to shattering seed in the field. A harvesting study conducted in west central Minnesota during 2001 and 2002 showed that

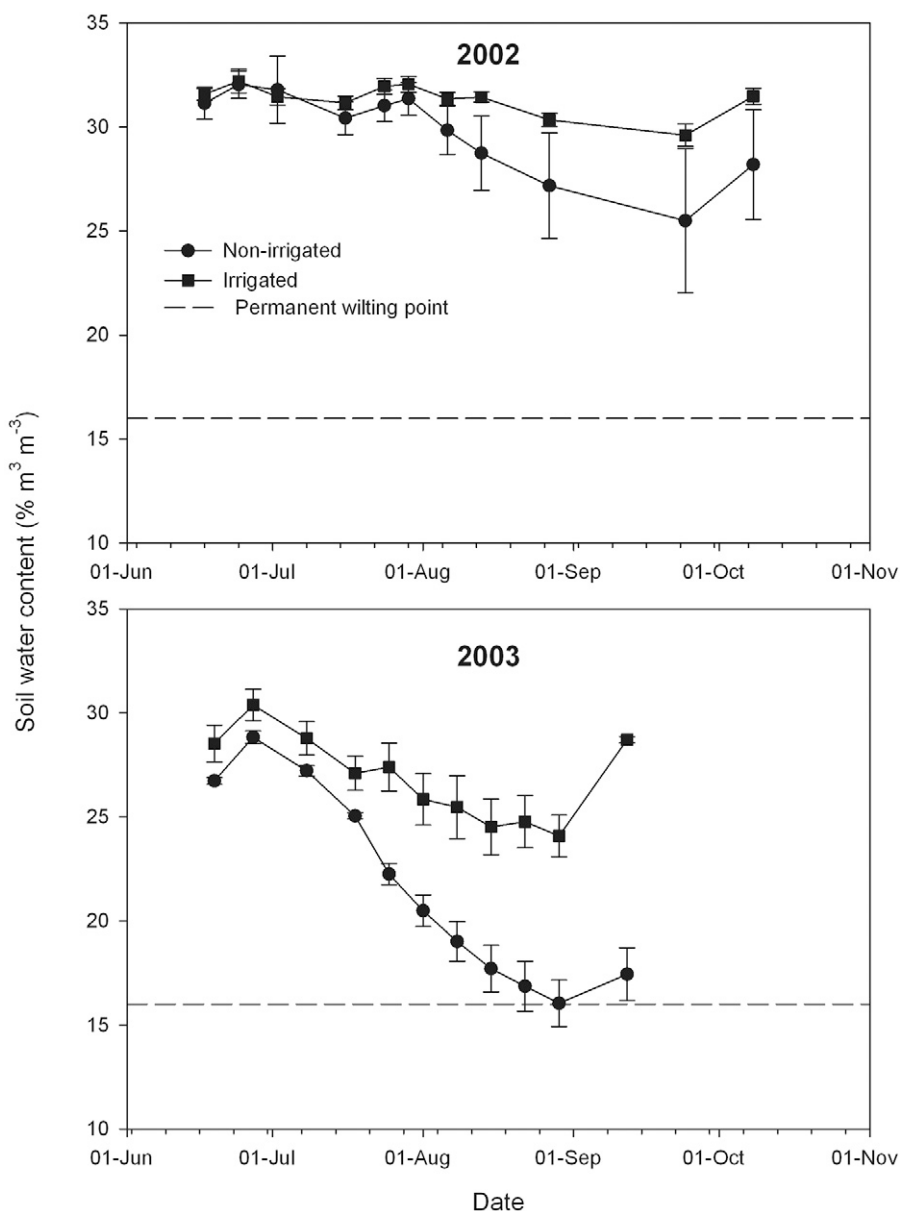


Figure 1. Soil water content in the upper 0.6 m of the soil profile from emergence to harvest, measured by neutron attenuation. Values are the mean \pm SE, $n = 3$, after averaging together the measurements at the 0.15- and 0.45-m depths for each date.

when sown in mid-May, cuphea seed yields were greatest when harvested during about a 2-wk period from mid- to late-September (Gesch et al., 2005). In this same study, cuphea that was left in the field until mid-October before harvesting lost 11 and 44% of its seed yield in 2001 and 2002, respectively, as a consequence of seed shattering. In the present study, cuphea was harvested 22 d later in 2002 (October 8) than in 2003 (September 16), and this may have allowed plants to lose more seed to shattering.

Cuphea (PSR23) flowers are strongly dependent on cross-pollination by insects, especially bumblebees (*Bombus* spp.), for fertility (Knapp and Crane, 2000). Differential availability of insect pollinators during reproductive growth could also have been a factor contributing to the differences in seed yield between 2002 and 2003, although

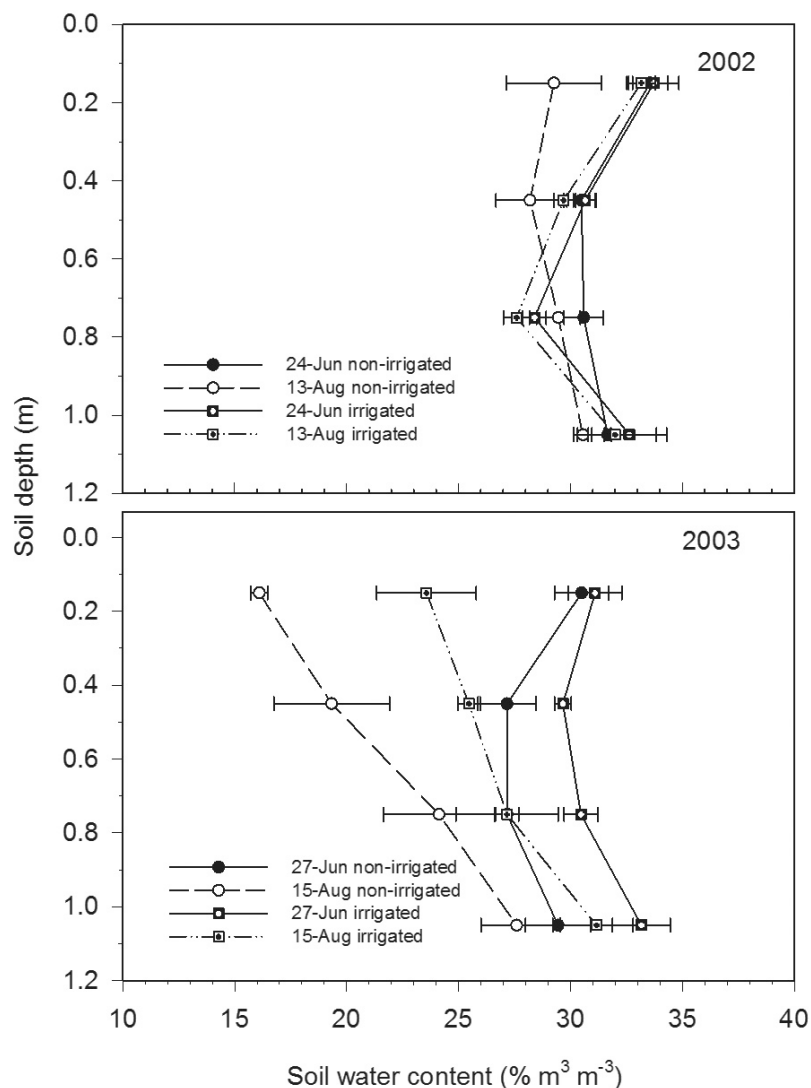


Figure 2. Soil water content as a function of soil depth in late June and mid-August for both irrigated and nonirrigated treatments. Values are means \pm SE, $n = 3$, and represent the mid-point of a 0.3-m depth interval.

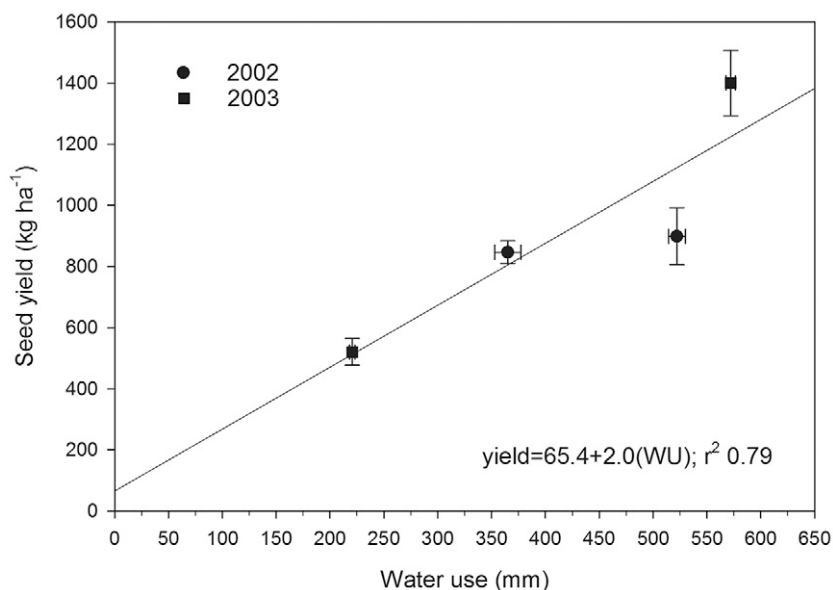


Figure 3. Cuphea (*Cuphea viscosissima* Jacq. \times *C. lanceolata* W.T. Aiton) seed yield as a function of water use (WU) for 2002 and 2003. Values are means \pm SE, $n = 3$.

this was not measured. Cuphea is also known to be susceptible to *Sclerotinia sclerotiorum* (Gulya et al., 2006). However, no symptoms of disease were observed in the present study.

Although WU was greater for irrigated than nonirrigated plants in 2003, WUE of seed production did not differ between treatments (Table 2). However, WUE of total biomass production was 54% greater for nonirrigated than irrigated plants. Our estimation of crop WU included the influence of soil water storage. Under drought, such as that experienced in 2003, WUE of biomass production often increases owing to reduced soil evaporation (Viets, 1966), whereas WUE of seed production generally decreases owing to adverse effects on reproductive growth.

Average WUE of seed production of 2.0 and 2.4 kg ha⁻¹ mm⁻¹ in 2002 and 2003 (Table 2), respectively, are slightly higher but similar to those reported by Sharratt and Gesch (2004) that ranged from 1.2 to 2.0 kg ha⁻¹ mm⁻¹ for cuphea grown under varied row spacing and planting dates. Values of WUE in this range are relatively low compared with other oilseed crops. For instance, Miller et al. (2003) reported that WUE ranged from 2.7 to 6.1 kg ha⁻¹ mm⁻¹ for canola (*Brassica napus* L.) and mustard (*B. juncea* L.) grown in the northern Great Plains on clay and silt loam soils, and Hattendorf et al. (1988) reported mean values for soybean [*Glycine max* (L.) Merr.] and sunflower (*Helianthus annuus* L.) of 5.5 and 4.4 kg ha⁻¹ mm⁻¹, respectively, grown on silt loam soils. Cuphea WUE, however, is similar to that of flax (*Linum usitatissimum* L.), which is around 2.0 kg ha⁻¹ mm⁻¹ (Berglund, 1995). Part of the reason for the low WUE of seed production for cuphea is its low harvest index (Table 2), which is generally lower than other more genetically refined crops such as soybean and suggests a need for future improvement.

Although total precipitation was similar between years, WU of nonirrigated plants from emergence to harvest was 144 mm less in 2003 than 2002. Conversely, irrigated plants in 2003 used 50 mm more water than those irrigated in 2002. This can be explained by the hot, dry conditions in 2003, leading to a relatively high evaporative demand. Only 29.2 mm of precipitation were received between 13 July and 8 September during eight rain events, with 9.9 mm being the most received on any day. During the month of August, cumulative ET_o and

vapor pressure deficit were 130 mm and 71.4 kPa, respectively, in 2003 as compared with 109 mm and 45.4 kPa in 2002. The additional WU of irrigated plants in 2003 was owing to greater soil water extraction to meet the increased evaporative demand, whereas there was insufficient soil water (Fig. 1) for nonirrigated plants to meet evaporative demand, resulting in lower WU than in 2002.

Within the range of crop WU of the study (212 to 578 mm), the relationship of seed yield to WU was linear, $r^2 = 0.79$ (Fig. 3). Using the regression equation in Fig. 3 and solving for WU gives $WU = (\text{yield} - 65.4)/2$, resulting in a WU intercept of -33 mm. The reason for the negative intercept is because of the values for the irrigated treatment in 2002, where WU, owing to the addition of irrigation, was higher than necessary to maximize yield, given other growth conditions for that season. Nevertheless, using the equation from Fig. 3 to estimate the WU to obtain 1000 kg ha⁻¹ seed yield, a relatively high but achievable yield for cuphea (Gesch et al., 2006), results in a WU of 467 mm (including soil water storage). Deriving the same relationship using WU and seed yield data from Sharratt and Gesch (2004) for cuphea in a WU range of 286 to 385 mm gives the equation $\text{yield} = 3.0(WU) - 456.7$; $r^2 = 0.74$ and, thus, a WU of 486 mm to produce a 1000 kg ha⁻¹ yield, a difference of only 19 mm from that estimated in the present study. Crop production (i.e., grain and/or dry matter yield) functions based on WU can be highly beneficial to producers for predicting the profitability of including a certain crop in their cropping systems (Nielsen et al., 2006). This is a first-time approximation of establishing a WU-crop production function for cuphea, and it should be cautioned that this may differ with soil type and climate, which will require further research.

Nonirrigated plants in 2003 began showing signs of drought stress by early August. Midday leaf photosynthesis and stomatal conductance of nonirrigated plants significantly decreased ($p < 0.05$) by early August (Fig. 4A), and by mid-August, photosynthesis was only 17% of that of irrigated plants. This was largely owing to the substantial reduction in stomatal conductance resulting from stomatal closure in response to drying conditions (Table 1 and Fig. 1) and reduced leaf water potential. Midday leaf water potential was significantly lower ($p < 0.05$) in nonirrigated plants by 25 July (Fig. 4B), which corresponded closely to when soil water content dropped below the 50% AWHC of nonirrigated soil (Fig. 1). By mid-August, when soil water content in nonirrigated plots was near the permanent wilting point, leaf water potential of nonirrigated plants was 56% less than leaves of irrigated plants (Fig. 4B). It was also noted that by early to mid-August, nonirrigated plants were exhibiting wilting and leaf rolling (field observation).

Stable isotope composition, $^{13}\text{C}/^{12}\text{C}$ (i.e., $\delta^{13}\text{C}$) can be used as an effective tool for assessing plant water relations (Bowling et al., 2008). For C_3 plants, such as cuphea,

discrimination of ^{13}C occurs through the processes of air diffusion into leaves and the photosynthetic carboxylation of CO_2 by Rubisco (Farquhar et al., 1989). Therefore, factors affecting CO_2 diffusion and carboxylation will cause $\delta^{13}\text{C}$ composition to vary. Drought, which leads to stomatal closure, tends to decrease discrimination, resulting in ^{13}C enrichment in C_3 plants (Gaudillere et al., 2002; Bowling et al., 2008). In the present study, determination of $\delta^{13}\text{C}$ in seed of nonirrigated cuphea further indicated the influence of drought stress during 2003. The $\delta^{13}\text{C}$ value was significantly ($p < 0.05$) greater for nonirrigated than irrigated plants (Fig. 5). Clearly, the water-deficit-related decline in photosynthetic assimilation was a major contributor to the lower seed and biomass yield of nonirrigated plants.

Despite relatively severe drought symptoms that occurred late in the summer of 2003, seed yield of nonirrigated plants was equal to or greater than yields reported in several other field studies (Gesch et al., 2005; Forcella et al., 2005; and Berti et al., 2008). In part, this might be related to cuphea's indeterminate flowering habit. Its long reproductive phase may allow seed development to occur before or after a period of summer drought when soil water is available. Before August in 2003, available soil moisture was likely great enough (Fig. 1) to not hinder seed set and filling between mid-July and early August, thus avoiding total crop failure. Alternatively, because plants had already entered reproductive phase (in mid-July) before showing drought symptoms (Fig. 4), sufficient remobilization and translocation of assimilate reserves may have been occurring to maintain reproductive growth, albeit less than irrigated plants. Also, any assimilate being fixed at the time drought was experienced may have been diverted from vegetative to reproductive growth. Phloem transport, the pathway for assimilate distribution in plants, tends to be resistant to water deficit, and grain crops such as wheat (*Triticum aestivum* L.) can transport assimilate unhindered to water deficit as low as -3.0 MPa (Turner and Burch, 1983).

Interestingly, seed mass and oil content of nonirrigated plants in 2003 were not affected by drought (data not shown), indicating that adequate assimilate was available and water relations were favorable enough to maintain maturation of developing seed. The physiological response of cuphea to drought is not well understood, and further research will be necessary to elucidate the impact of drought on yield and its components, especially when imposed at different stages of growth and development.

CONCLUSIONS

Obviously, in a dry year such as experienced in 2003, cuphea was highly responsive to supplemental water applications through irrigation. However, in 2002 when near to above-average precipitation was received during the critical growing months of July and August, (and soil moisture was not depleted below 60% of the available soil water

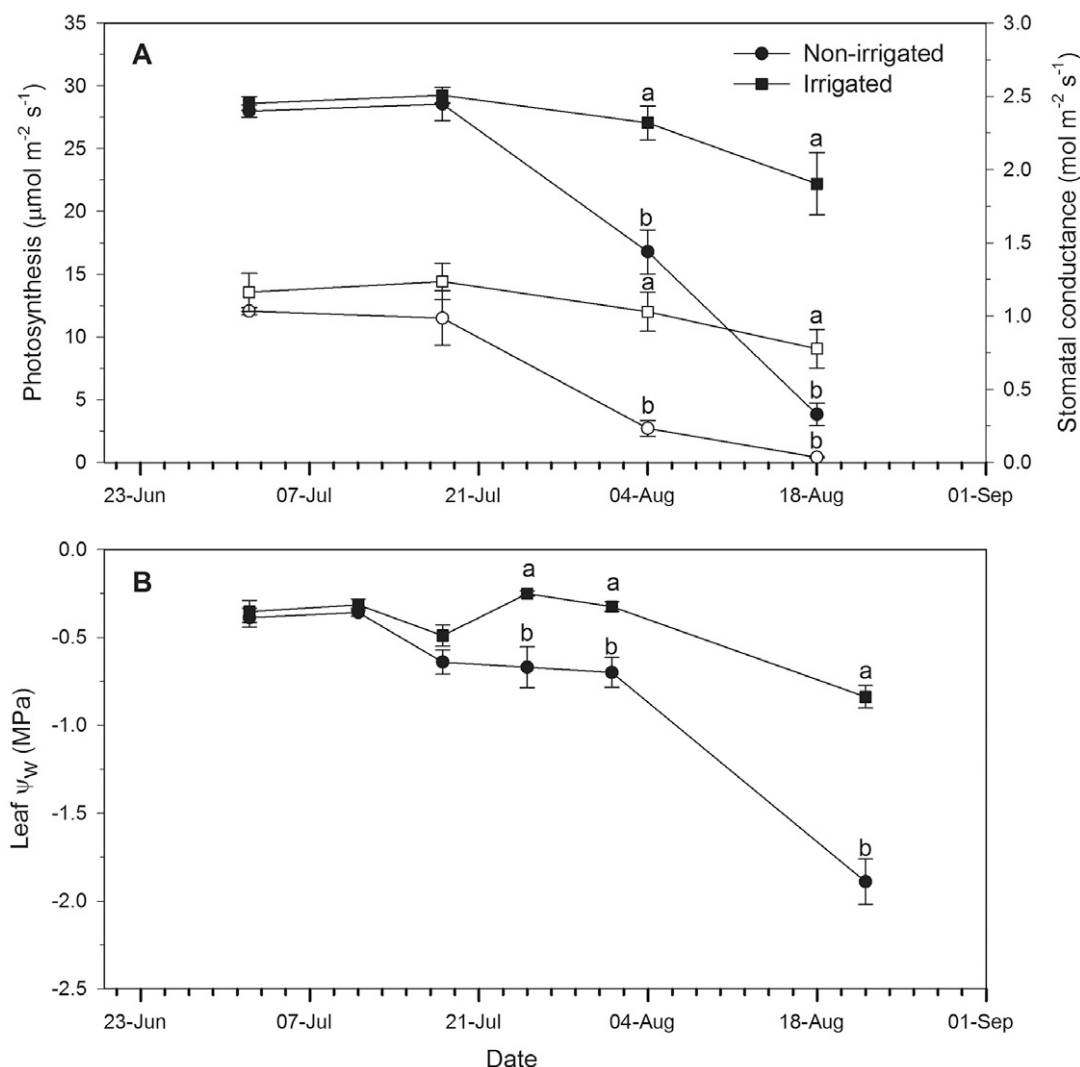


Figure 4. (A) Leaf photosynthesis (closed symbols) and stomatal conductance (open symbols) and (B) leaf water potential during the 2003 growing season for irrigated and nonirrigated cuphea (*Cuphea viscosissima* Jacq. \times *C. lanceolata* W.T. Aiton). Values are means \pm SE, $n = 3$, for 4A and 4B. Different letters between treatments for the measured attribute at a given date denote significant differences at the $P \leq 0.05$ level.

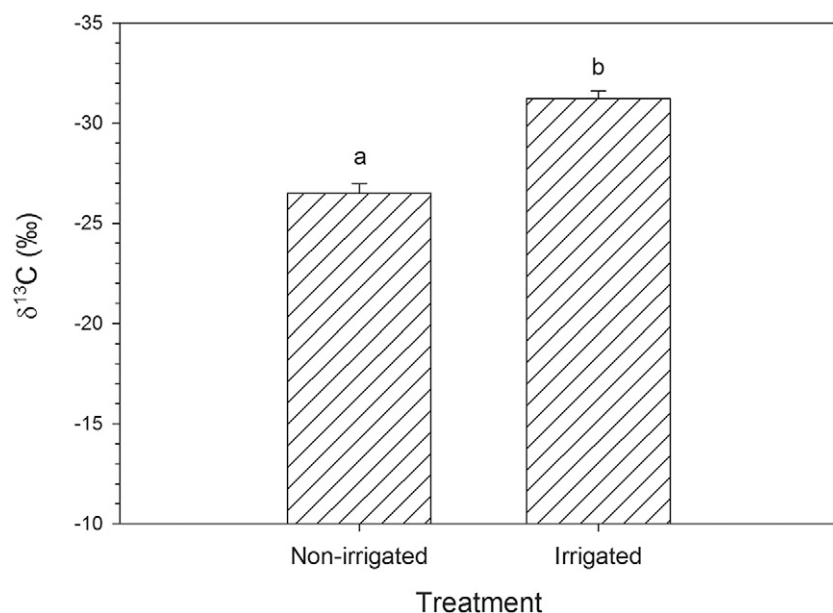


Figure 5. Comparison of $\delta^{13}\text{C}$ of irrigated and nonirrigated cuphea (*Cuphea viscosissima* Jacq. \times *C. lanceolata* W.T. Aiton) during 2003. Values are the mean \pm SE, $n = 3$. Different letters denote a significant difference at the $P \leq 0.05$ level.

holding capacity) additional irrigation had no effect on seed yield and growth of cuphea. Because cuphea is susceptible to drought stress, more research will be needed to optimize irrigation of cuphea in regions where there is periodic drought, especially when it coincides with the reproductive phase of plants. Depending on soil properties, additional water in the form of irrigation will be needed in areas receiving less than 400 mm of precipitation during the growing season to optimize cuphea yield.

Until cultivars are developed with improved WUE, cuphea (PSR23) is best suited for production in areas with relatively high annual precipitation and soils not prone to drought. A better understanding of cuphea's WU response under different soil types and climate is needed, as is a more thorough understanding of its physiological response to drought stress.

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